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Evaluation of lakewide, early season herbicide treatments for controlling invasive curlyleaf pondweed (*Potamogeton crispus*) in Minnesota lakes

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Abstract

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Curlyleaf pondweed (*Potamogeton crispus*) is a nonnative aquatic plant found throughout temperate regions of North America. Its early season growth, propensity to form dense surface mats, and ability to out-compete native aquatic plants allow it to degrade the ecological and recreational quality of many lakes. Consequently, there is great interest in adopting lakewide management strategies that can reduce the negative impacts of curlyleaf and provide long-term control. We collaborated with the Minnesota Department of Natural Resources from 2006 through 2009 to evaluate lakewide, early season herbicide treatments for controlling curlyleaf. Nine curlyleaf-infested lakes were treated with endothall at 0.75–1.00 mg active ingredient per liter (ai/L) or fluridone at 2–4 $\mu\text{g ai/L}$ (only one lake treated with fluridone) for up to 5 consecutive years. Three additional infested lakes were selected to serve as untreated reference lakes. In each year we assessed the frequency and biomass of curlyleaf (May and Jun), documented the production of new curlyleaf turions on standing plants (Jun), and tracked changes in the abundance and viability of turions in lake sediments (Oct). We found that herbicide treatment inhibited turion production and substantially reduced curlyleaf frequency, biomass, and sediment turion abundance in treated lakes. The largest reductions of curlyleaf frequency, biomass, and turion abundance occurred in the initial 2–3 years of treatment, with less substantial reductions in the subsequent years of treatment. Despite these reductions, viable turions remained in the sediments of treated lakes after up to 5 consecutive years of treatment. These results suggest that although lakewide, early season herbicide treatments can effectively control curlyleaf, inhibit turion production, and reduce the abundance of turions in sediments, ongoing management will likely be required to maintain long-term control.

Key words: curlyleaf pondweed, endothall, fluridone, lakewide, *Potamogeton crispus*, turions

Curlyleaf pondweed is a nonnative, submersed aquatic plant that has become a widespread nuisance in temperate regions of North America (Catling and Dobson 1985, Bolduan et al. 1994). Curlyleaf's ability to dominate the plant community in northern lakes is enhanced by its novel life cycle (Tobiessen and Snow 1984). Although it is considered a perennial species, it behaves as a winter annual in northern lakes (Netherland et al. 2000, Madsen and Crowell 2002), sprout-

ing from turions in the fall, growing rapidly in the early spring (Kunii 1982, Tobiessen and Snow 1984, Nichols and Shaw 1986), and forming new turions and dense surface growth in May and June (Wehrmeister and Stuckey 1992, Bolduan et al. 1994). Stands of curlyleaf typically senesce by midsummer, depositing any newly produced turions to the sediment. In addition to depositing new turions, this rapid senescence and subsequent decay of curlyleaf may contribute to nutrient recycling in infested lakes (Bolduan et al. 1994, James et al. 2002). Although curlyleaf also produces seeds, under most conditions its annual life cycle

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is almost entirely dependent on sprouting from turions in lake sediments (Rogers and Breen 1980, Sastroutomo 1981, Bolduan et al. 1994). Consequently, there is great interest in adopting management strategies that can prevent turion production on a lakewide scale and deplete accumulated turions, thus decreasing nuisance growth and the need for intensive management in subsequent years (Netherland et al. 2000).

Curlyleaf growth and turion production have been controlled in mesocosm tank studies with low-dose herbicide treatments (Netherland et al. 1997, 2000, Poovey et al. 2002, Skogerboe and Getsinger 2002, Poovey et al. 2005, 2006), specifically using fluridone herbicide (1-methyl-3-phenyl-5-[3-(trifluoromethyl)phenyl]-4(1H)-pyridinone) and endothall herbicide (7-oxabicyclo[2.2.1]heptane-2,3-dicarboxylic acid). Furthermore, these tank studies and additional work by Woolf and Madsen (2003) suggested that treatments could be conducted in the early spring to take advantage of curlyleaf's active, early season growth, potentially reducing impacts to native plants that do not grow actively until later in the season (Barko et al. 1982).

Recent evaluations of early season, low-dose herbicide treatments in lakes have shown dramatic reductions in curlyleaf biomass within each year of treatment and decreased recurrence of curlyleaf sprouting after multiple consecutive years of treatment (Skogerboe et al. 2008). Although these results imply that herbicide treatments reduced the number of curlyleaf turions in lake sediments, turion production and the abundance of turions were not directly measured in these evaluations. A more complete understanding of the effects of early season herbicide treatments on curlyleaf growth, tu-

tion production, and the abundance and viability of turions in lake sediments is needed to further evaluate the effectiveness of early season treatments for managing curlyleaf.

We collaborated with the Minnesota Department of Natural Resources (MNDNR) from 2006 through 2009 to evaluate the effectiveness of lakewide, early season, low-dose herbicide treatments for managing curlyleaf in Minnesota lakes. The specific objectives of our project were to determine (1) if early season, low-dose herbicide treatments reduced curlyleaf frequency and biomass within the year of treatment; (2) if curlyleaf frequency and biomass decreased from year to year with consecutive annual treatments; (3) if the production of new curlyleaf turions was reduced by treatment; and (4) if the abundance and viability of turions in sediments were reduced by multiple consecutive years of treatment. A companion paper (Jones et al. 2012) assesses the effects of the treatments on native aquatic plants in our study lakes.

Study sites

The MNDNR selected 9 Minnesota lakes to receive lakewide, early season endothall or fluridone treatments in multiple consecutive years to control nuisance curlyleaf pondweed growth (Table 1; Fig. 1). We selected 3 additional curlyleaf-infested lakes to serve as untreated reference lakes during the study to assess whether any observed changes in treated lakes were larger than natural background variation. All 12 of these study lakes were located in east-central Minnesota between 44°N and 47°N (230 km north-south distance; Fig. 1) and represented a range of trophic states

Table 1.—Study lake attributes, herbicide application details, and pretreatment conditions. Untreated reference lakes shown in bold.

Lake	MN Lake ID	Herbicide ^a	Years Treated	Secchi ^b (m)	Area (ha)	% Littoral ^c	% Littoral Infested ^d
Coal	77-0046	None	—	2.4	69	40	45
Rebecca ^e	27-0192	None/E	2009	1.9	105	50	95
Vails	73-0151	None	—	1.6	64	80	75
Blueberry	80-0034	E	2007-2009	0.8	211	100	45
Clear	47-0095	E	2007-2009	0.6	201	100	70
Crookneck	49-0133	E	2006-2008	2.9	74	80	40
Fish	70-0069	E	2005-2008	1.6	70	40	60
Julia	71-0145	E	2006-2009	0.6	62	100	50
Long	30-0072	E	2007-2009	1.0	158	100	60
Lower Mission	18-0243	E	2006-2009	3.8	292	60	60
Rush	71-0147	E	2006-2009	0.6	65	100	80
Weaver	27-0117	F/E ^f	2005-2009	2.3	62	50	80

^aE = endothall (0.75 to 1.00 mg ai/L), F = fluridone (2 to 4 µg ai/L)

^bPretreatment Secchi depth (May–September mean), Minnesota Pollution Control Agency

^c% Littoral calculated as [(area of lake ≤4.6 m ÷ total lake surface area) × 100%]

^d% Littoral Infested is maximum littoral % occurrence of curlyleaf pondweed from all available surveys

^eUntreated reference from 2006 to 2008, treated with endothall in 2009

^fTreated with fluridone in 2005, 2006, and 2007, and with endothall in 2008 and 2009

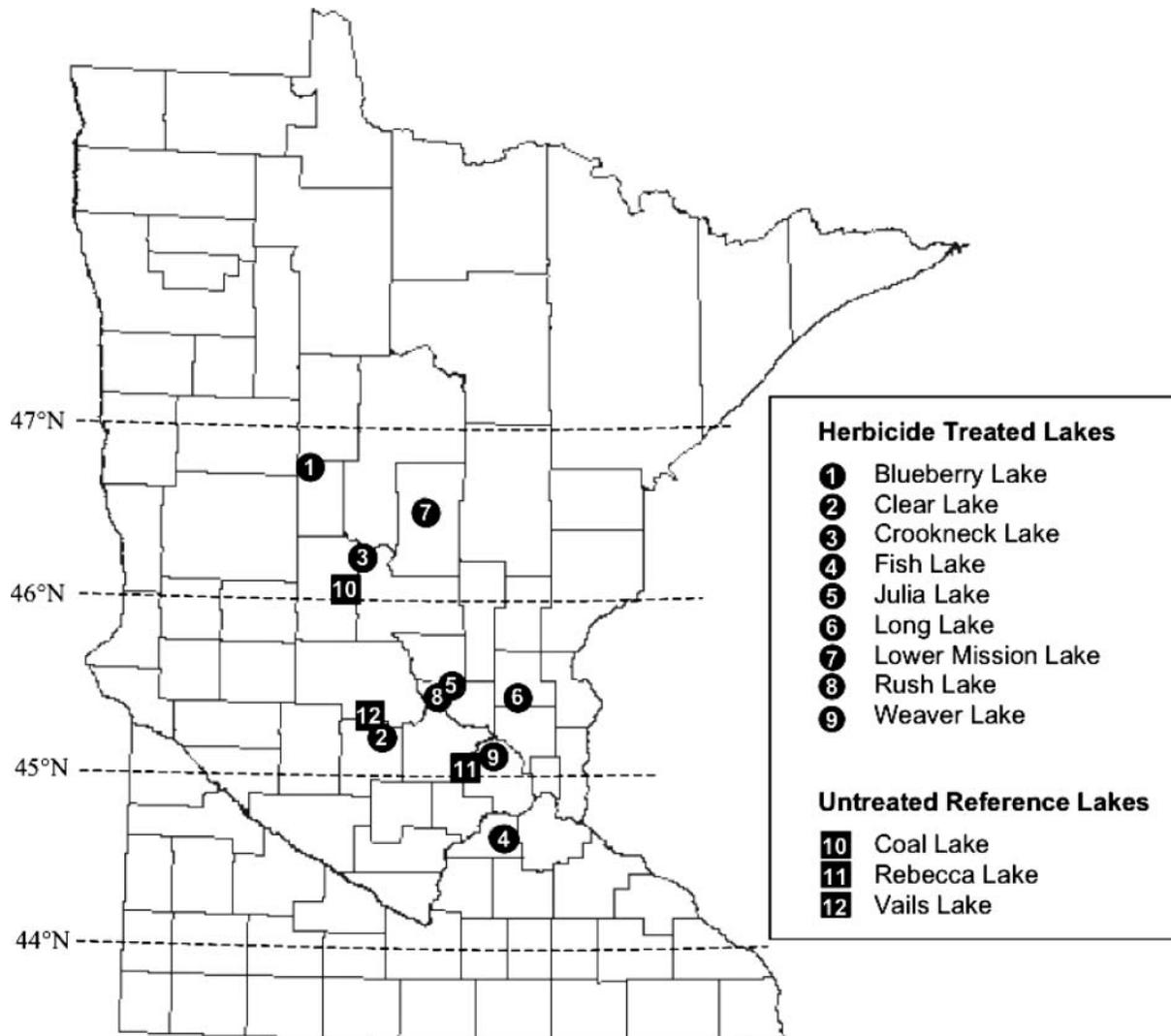


Figure 1.—Locations of the 9 herbicide-treated lakes (●) and 3 untreated reference lakes (■) in Minnesota.

(mesotrophic to hypereutrophic) and degrees of pretreatment curlyleaf infestation (40–80% littoral area infested; Table 1).

Materials and methods

Herbicide treatments

Treated lakes received early season, low-dose applications of herbicide annually for up to 5 consecutive years between 2005 and 2009 (Table 1). Areas of curlyleaf growth in each treated lake were delineated just prior to each treatment and the MNDNR supervised herbicide applications. The initial year of treatment was not synchronized across our study lakes and ranged from 2005 to 2009 (Table 1). Of the 9 treated lakes, 8 were treated exclusively with en-

dothall, and one (Weaver Lake) was treated with fluridone from 2005 to 2007 before being switched to treatment with endothall in 2008 and 2009 to allow recovery of coontail (*Ceratophyllum demersum*), which had declined in Weaver Lake during the years of fluridone treatment. All herbicide treatments were intended to control curlyleaf lakewide. For endothall treatments, this was achieved by treating only those areas where the most recent spring delineation survey found curlyleaf (lakewide treatment). For the fluridone treatment (Weaver), the entire mixed volume of the lake was dosed (true whole-lake treatment). In the final year of our study (2009), 2 of the previously treated lakes (Fish and Crookneck) were not treated, and one of the 3 reference lakes (Rebecca) was treated with endothall. Consequently, in 2009 our study included 8 treated lakes and 2 reference lakes.

All herbicide applications were conducted using a boat-mounted tank injection system with 1 m drop hoses to allow precise dosing and coverage. For endothall treatments, a liquid formulation of the dipotassium salt of endothall was applied when surface water temperatures were between 10 and 15 C. The rate of endothall application was adjusted based on the water depth at treated locations to achieve a target concentration of 0.75–1.00 mg active ingredient per liter (ai/L) within the treated areas; however, in-lake endothall concentrations were not monitored. For fluridone treatments, liquid fluridone was applied uniformly over several widely spaced, open-water transects at a rate sufficient to achieve a lakewide target concentration of 2–4 μg ai/L once fully mixed into the observed epilimnetic volume of the lake (true whole-lake treatment). Fluridone concentrations were periodically measured in the weeks following application using an enzyme-linked immunosorbent assay (FastTEST) developed by SePRO Corporation (Carmel, IN; Netherland et al. 2002). If needed, fluridone was applied a second time to maintain the target concentration for at least 60 d.

Assessment of curlyleaf frequency

We conducted point-intercept aquatic vegetation surveys (Madsen 1999) on each lake in May and June of each year. For each lake, we generated a minimum of ~100 littoral sample points (MNDNR defined littoral area; ≤ 4.6 m depth) using desktop ArcGIS or ArcView GIS software (ESRI, Redlands, CA) and the MNDNR Garmin extension (Minnesota Department of Natural Resources, St. Paul, MN). These points were arranged in a regularly-spaced grid (50–80 m spacing between points), with a greater number of sample points on lakes with more littoral area or more complex shorelines. We sampled vegetation at each designated point with one toss of a 0.33 m wide, weighted, double-headed rake attached to a rope. On each toss, the rake was dragged for approximately 3 m while in contact with lake sediments to sample vegetation in an area of approximately 1 m² at each location. Retrieved plants were inspected in the field, and all occurrences of curlyleaf pondweed were recorded. We then calculated curlyleaf frequency (% occurrence) for each survey on each lake by dividing the number of sampled littoral locations where curlyleaf was found by the total number of littoral sites sampled (≤ 4.6 m). We also recorded occurrences of any other aquatic plant taxa encountered during the May and June surveys, and conducted a third survey in August of each year to further assess effects of treatments on native plant taxa. A separate study (Jones et al. 2012) evaluates effects on native plants in the endothall-treated lakes.

Assessment of curlyleaf biomass

We used a boat-based vertical rake method (Johnson and Newman 2011) to collect biomass at approximately 40 locations during each point-intercept plant survey. Biomass sample locations were randomly selected from the point-intercept survey points using desktop ArcView GIS software and the Minnesota DNR Random Sample Generator extension for ArcView. At each selected location, we lowered a 0.33 m wide, 14-tine, single-headed rake vertically until the rake head reached the lake sediment. We then rotated the rake on its axis 3 full turns and retrieved it vertically while continuing to turn it slowly to prevent the loss of collected plant fragments. Each sample collected plants from approximately 0.09 m² of sediment. Upon retrieval, we rinsed off any sediment, placed all collected plants into a labeled plastic bag, drained excess water, and stored the samples at 5 C until they could be processed. In the lab, curlyleaf in each sample was sorted from other taxa, and roots and rhizomes were removed and discarded. Sorted curlyleaf plants were then washed, dewatered in a salad spinner, dried for at least 48 h at 105 C, and weighed. We also assessed biomass of any other aquatic plant taxa found in biomass samples from May, June, and August of each year (results presented in Jones et al. 2012). We calculated curlyleaf biomass (dry g/m²) by dividing the dry mass of each sample (shoots + attached turions) by the rake sample area (0.09 m²).

Assessment of curlyleaf turions

We estimated the annual production (number and biomass) of new curlyleaf turions in each lake by assessing turions attached to plants collected in the June curlyleaf biomass samples. Turions were manually sorted from dried biomass samples, counted, redried at 105 C for 24 h, and weighed. Counts of newly produced turions in each sample were divided by the sampled area (0.09 m²) to yield turion production in turions/m². We then calculated mean littoral turion production (turions produced/m²) for each lake and year.

In the fall of each year (Oct), we measured the abundance of curlyleaf turions in littoral sediment samples collected from each lake. We used a petite Ponar dredge (225 cm² basal area; sample depth ~10 cm) to collect one sediment sample at each of the same 40 locations where biomass was collected (May biomass locations for treated lakes; June biomass locations for reference lakes). Upon retrieving each sediment sample, we removed any material from the outside of the closed dredge, emptied the sampler contents into a sifting bucket (1 mm screen), and gently sifted the sample in the field to remove fine sediment. The contents remaining in the bucket after sifting were placed into a labeled plastic bag and stored in a cooler while in the field. In the lab, we manually sorted turions from other debris and recorded

total turion counts for each sample. Small turion fragments (those that did not include a portion of a central turion stem) and severely decayed turions (those that did not retain their shape when lightly squeezed) were discarded and were not included in the final turion counts; sprouting tests indicated that these fragments and soft turions were not viable. We calculated turion abundance at each sampled site (N of turions \div 0.0225 m^2 ; N/m^2) and mean littoral turion abundance for each lake in each year.

We also assessed the viability of turions collected in sediment samples from each lake in each year. Turions found to be sprouted at the time of sample processing were tallied as viable and then discarded. Remaining unsprouted turions from each lake were placed into clear sealable plastic bags with a small amount of water and stored in the dark at 5 C for 30 d to simulate typical fall conditions in surface sediments of Minnesota lakes to break turion dormancy (Sastroutomo 1981). During this period of cold storage, bagged turions were inspected weekly, and any sprouted turions were tallied and discarded. After this period of cold storage, remaining unsprouted turions were incubated for an additional 90 d at 20 C with 14 h of light per day from a bank of 4 fluorescent 20-watt grow lamps. Two different methods of warm incubation were used. In 2006, turions were incubated in shallow trays with 1 cm of sandy sediment and 3 to 5 cm of water. After several weeks of warm incubation, many of the trays became covered with dense filamentous algae that made it difficult to assess sprouting. Consequently, in subsequent years, turions were incubated in sealed clear plastic bags with a small amount of water, little air-space, and no sediment; this reduced the amount of algae growth and made assessments of sprouting easier. During the period of warm incubation, samples were inspected every 2 weeks, and sprouted turions were tallied and discarded. After 90 d of warm incubation, we calculated final turion viability (proportion sprouted) by dividing the total number of sprouted turions (in-lake + cold-storage + warm incubation) by the total number of turions collected (sprouted + unsprouted) from each lake, and calculated the abundance of viable turions (turion abundance \times proportion sprouted; N/m^2) in each lake for each year.

Statistical analyses

We evaluated within-year changes (May to Jun) of curlyleaf frequency in each lake using chi-square (Zar 2010) and within-year changes of curlyleaf biomass with an unpaired, 2-sample Welch's t-test (no assumption of equal variance between groups; Welch 1947, Zar 2010).

For between-year comparisons of curlyleaf frequency and biomass, we focused on May data (collected prior to treatment in each year) to assess the degree of curlyleaf control that carried over from previous years of treatment (May

to May). We anticipated that June frequency and biomass would be affected greatly by treatments within each year, making it difficult to discern any carryover effects from previous years of treatment. By contrast, May data were collected just prior to each year's herbicide treatment, so any between-year decreases in May frequency or biomass that were significantly greater than seen in the May data from reference lakes would suggest carryover effects from the previous year of treatment. For between-year comparisons of curlyleaf turion abundance (collected only once each year), we used the Welch's t-test.

The initial year of treatment was not synchronized across all of the treated lakes (Table 1). Consequently, we grouped results from treated lakes by the number of years treated rather than by calendar year. This aligned the first year of treatment (and subsequent years) across all of our treated lakes and allowed us to evaluate changes in the treated lakes based on the number of years treated (Y1, Y2, etc.; henceforth referred to as "treatment years"). Due to the asynchrony of the initial treatment year (Y1) among the study lakes, however, treatment years did not align with calendar years across lakes. Consequently, we were not able to compare means from individual treatment years to individual years in reference lakes. Instead, we compared the means across the treated lakes in each treatment year to the 4-year mean across all reference lakes using an unpaired, 2-sample Welch's t-test. We also used the Welch's t-test to compare means in each treatment year to the pretreatment (Y0) means in the treated lakes. In addition, we used regression analysis to evaluate the relationship between curlyleaf shoot biomass and turion production in reference lakes. All analyses were conducted using R statistical software (R Development Core Team 2008).

Results

Curlyleaf frequency

When grouped by treatment year, there was a clear trend of decreasing May curlyleaf frequency in the treated lakes with successive years of treatment, particularly after 2 years of treatment (Fig. 2). After 1 year of treatment, May curlyleaf frequency in the treated lakes ($Y1 = 57\% \pm 9\%$ occurrence; mean ± 2 SE, used henceforth) remained similar to the 4-year mean May curlyleaf frequency in the reference lakes ($54\% \pm 13\%$ occurrence, $P = 0.74$) and was not different than the mean pretreatment May curlyleaf frequency in treated lakes ($Y0 = 56\% \pm 12\%$ occurrence, $P = 0.91$). In the subsequent years of treatment, however, May curlyleaf frequency in treated lakes was consistently lower than the 4-year mean May frequency in reference lakes ($P \leq 0.01$) and was lower than the pretreatment May frequency in treated lakes ($Y2 = 30\% \pm 10\%$ occurrence, $P = 0.003$; $Y3 = 16\% \pm 12\%$, $P < 0.001$; $Y4 = 8\% \pm 12\%$, $P = 0.01$).

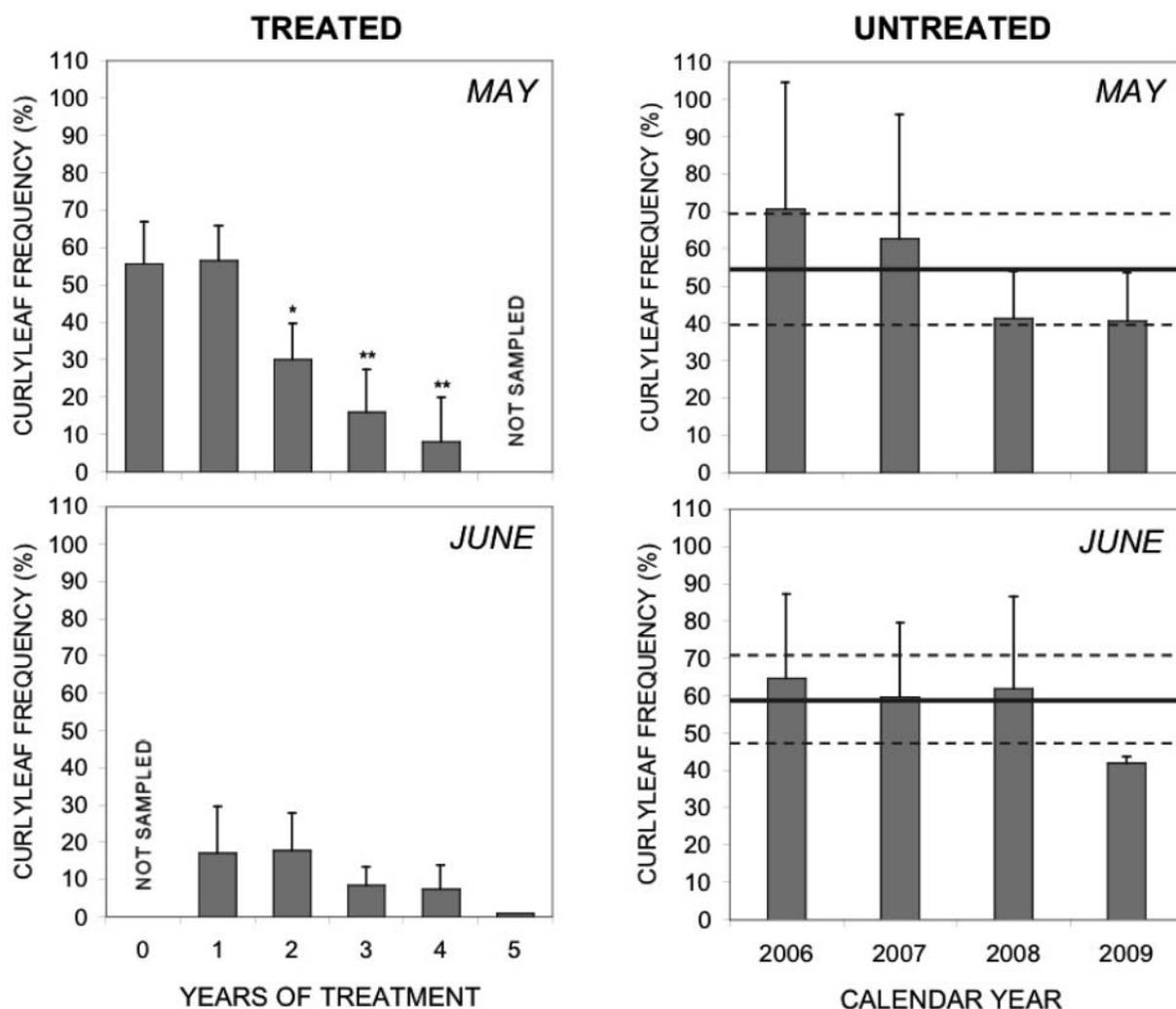


Figure 2.—Mean curlyleaf frequency (% occurrence; May and Jun) in littoral area (≤ 4.6 m) of treated lakes (by years of treatment) and untreated reference lakes (by calendar year). Error bars represent $+2$ SE. Significant reductions in treated lakes relative to pretreatment (year 0) indicated by “*” for $P < 0.05$ and “**” for $P < 0.01$ (Welch’s t-test). Horizontal lines represent the 4-year mean (solid) and 95% CI (dashed) for untreated reference lakes. May data from treated lakes were collected immediately before treatment, and June after treatment in each year, consequently May data are associated with the previous year of treatment.

June curlyleaf frequency in the treated lakes was consistently lower than seen in May and was consistently much lower than the 4-year mean June curlyleaf frequency in the reference lakes (Fig. 2 and 3), indicating strong within-year effects of treatments on curlyleaf frequency. Looking at individual lake responses (Fig. 3), curlyleaf frequency in treated lakes decreased between May and June (chi-squared; $P < 0.05$) after 23 of the 28 lake treatments, with the remaining 5 cases showing no significant within-year change in curlyleaf frequency (remained low) after treatment. By contrast, curlyleaf frequency in the reference lakes increased ($P < 0.05$) or remained high between May and June in 8 of the 11 cases. In the remaining 3 cases (Rebecca Lake in 2006 and 2007, and Vails Lake in 2006), curlyleaf frequency de-

creased between May and June ($P < 0.05$) but remained high ($>70\%$ occurrence in Rebecca; $>40\%$ occurrence in Vails). Frequency varied greatly among reference lakes (45–85%), but was fairly consistent within each reference lake over the 4 years of the study (Fig. 3). Curlyleaf frequency in the reference lakes was less variable in June than in May, suggesting that June frequency was affected less by early season weather conditions than May frequency.

Curlyleaf biomass

When grouped by treatment year, there was no trend of decreasing May curlyleaf biomass in the treated lakes with successive years of treatment (Fig. 4). Pretreatment May

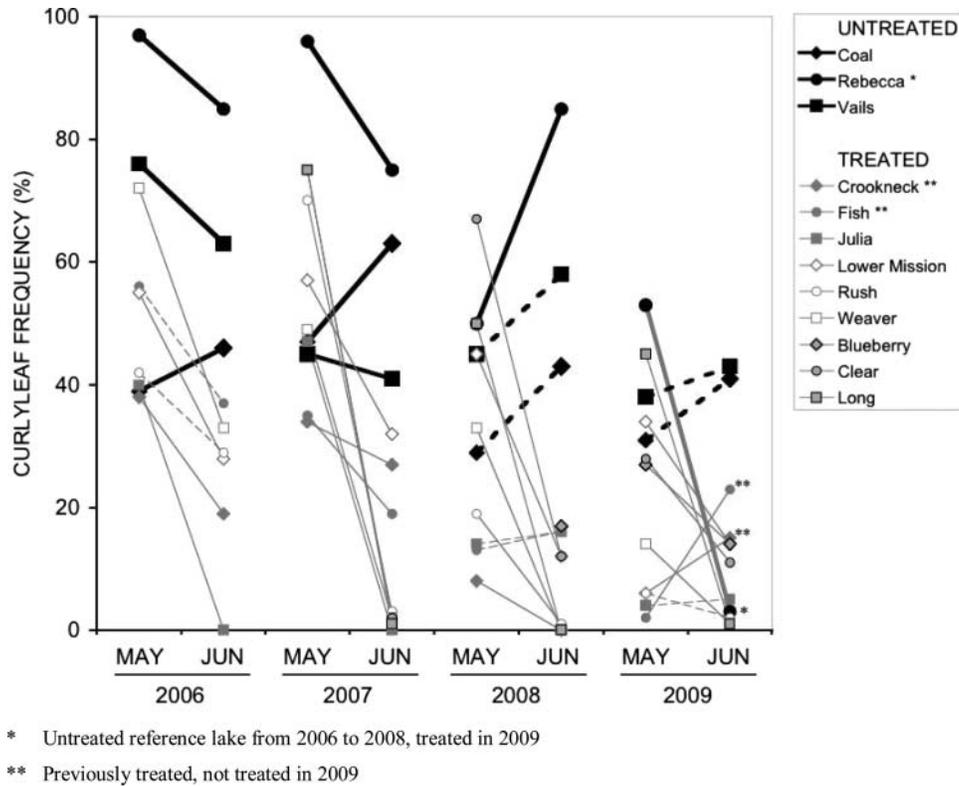


Figure 3.—Curlyleaf pondweed frequency (% occurrence) in littoral area (≤ 4.6 m) of untreated reference lakes (black lines) and herbicide-treated lakes (gray lines) in May and June of each calendar year. Significant within-year changes in frequency ($P < 0.05$, chi-square) are indicated by solid lines, and nonsignificant changes by broken lines.

biomass (Y_0) in treated lakes was very low (2 ± 2 dry g/m^2) and was similar to the May biomass in treated lakes over the subsequent years of treatment. In each treatment year, however, May biomass in the treated lakes was consistently much lower ($P < 0.02$) than the 4-year mean May biomass in the reference lakes (42 ± 23 dry g/m^2), suggesting that treatments had some carryover effects upon curlyleaf biomass (suppression).

June curlyleaf biomass remained low in the treated lakes (< 10 dry g/m^2 ; Fig. 4 and 5) and was consistently much lower ($P \leq 0.005$) than the 4-year mean June biomass in the reference lakes (143 ± 78 dry g/m^2), indicating strong within-year effects of treatments on curlyleaf biomass. Looking at individual lake responses (Fig. 5), curlyleaf biomass in treated lakes decreased between May and June ($P < 0.05$) after 11 of the 28 lake treatments, with the remaining 17 cases showing no significant within-year changes in biomass after treatment (remained low). By contrast, curlyleaf biomass in the reference lakes increased or remained stable between May and June and was generally > 40 g/m^2 . Curlyleaf biomass in the reference lakes was more variable than curlyleaf frequency, both among lakes and between years.

Curlyleaf turions

Turion production was much lower in treated lakes (0.7 ± 0.8 turions/ m^2) than in reference lakes (451 ± 311 turions/ m^2 , $P < 0.02$) over the 4 years of the study (Table 2). The mean number of turions produced per square meter in treated lakes was only 0.2% of the mean turion production observed in reference lakes. The number of turions produced at individual sampling sites in reference lakes was strongly related to curlyleaf shoot biomass ($R^2 = 0.8$; Fig. 6). Regression of turion production (turions/ m^2) against June curlyleaf shoot biomass from untreated reference lakes showed that roughly 3 turions (2.9 ± 0.2 turions) were produced for every gram (dry) of curlyleaf shoot biomass. On average, dry turion biomass accounted for $9\% \pm 1\%$ of total dry curlyleaf biomass (shoots + turions) in reference lakes, with a mean individual turion mass of 43 ± 1 dry $mg/turion$.

The abundance of turions in sediments of the treated lakes in each treatment year was consistently lower ($P < 0.03$) than the 4-year mean turion abundance in the reference lakes (Fig. 7). Pretreatment turion abundance data were available for only 2 of our study lakes (Weaver and Rebecca). Consequently, we were not able to evaluate reductions of turion abundance that may have occurred during the initial year

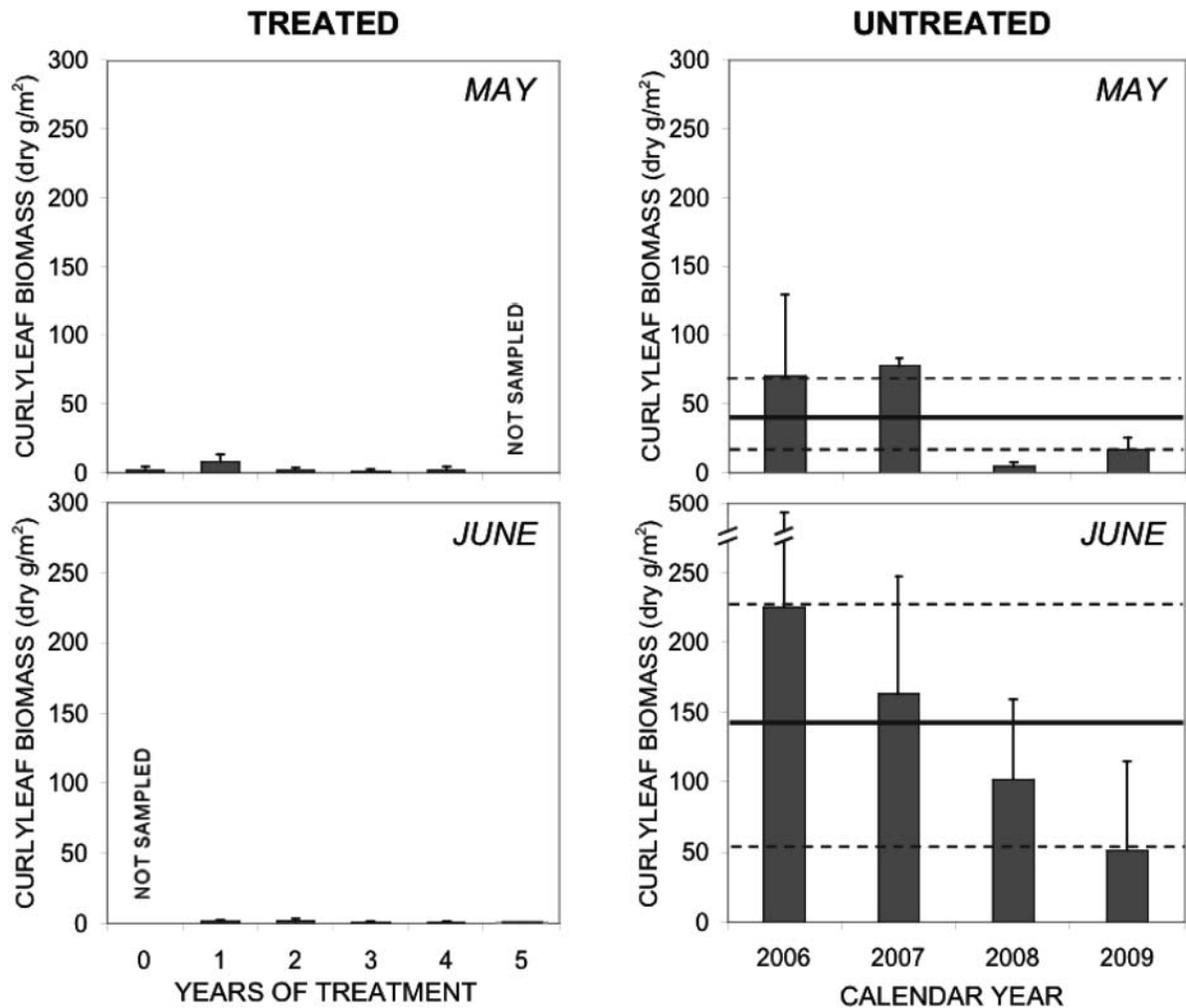
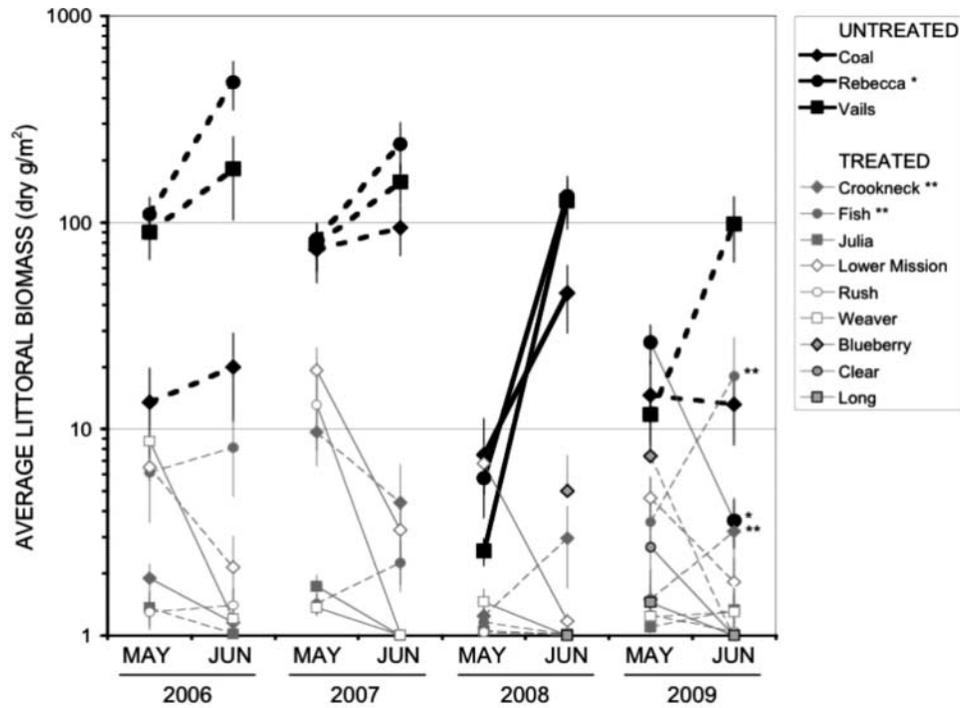


Figure 4.—Mean curlyleaf biomass (dry g/m², May and Jun) in littoral area (≤ 4.6 m) of treated lakes (by years of treatment) and untreated reference lakes (by calendar year). Error bars represent +2 SE. Horizontal lines represent the 4-year mean (solid) and 95% CI (dashed) for untreated reference lakes. May data from treated lakes were collected immediately before treatment, and June after treatment in each year, consequently May data are associated with the previous year of treatment.

of treatment for all of the treated lakes. However, the available pretreatment data showed that in Weaver Lake, turion abundance decreased by 51% ($P = 0.01$) in the first year of treatment, from 426 ± 140 turions/m² in 2004 to 207 ± 68 turions/m² in 2005 (Fig. 8). Similarly, in Rebecca Lake, turion abundance decreased by 49% ($P = 0.02$) in the first year of treatment, from 853 ± 292 turions/m² in 2008 to 434 ± 214 turions/m² in 2009. Although we did not have pretreatment data for the remaining study lakes, we observed substantial decreases in turion abundance ($P < 0.05$) between the first and second year of treatment in 3 additional treated lakes (77% reduction in Fish, 64% in Blueberry, and 72% in Long). This strongly suggests that treatments substantially decreased turion abundance in the initial 2 years of treatment; however, we observed only minor additional

decreases in turion abundance in lakes that were treated for more than 2 years (Fig. 8).

In the reference lakes, turion abundance was highly variable both among lakes and between years over the 4 monitored years (Fig. 7 and 8). Rebecca Lake had consistently high turion abundance (650–850 turions/m²), Coal Lake had consistently lower turion abundance (120–230 turions/m²), and Vails Lake had intermediate turion abundance that was highly variable between years (110–770 turions/m²). This large between-year variability of turion abundance in reference lakes seemed to be attributable to annual differences in turion production, and was likely due to differences in weather and in-lake conditions in each year. By contrast, after the initial 2 years of herbicide treatment, turion



* Untreated reference lake from 2006 to 2008, treated in 2009
 ** Previously treated, not treated in 2009

Figure 5.-Mean curlyleaf pondweed dry biomass (shoots + attached turions, dry g/m²) in littoral area (≤4.6 m) of untreated reference lakes (black lines) and herbicide-treated lakes (gray lines). Error bars represent ±1 SE. Significant within-year (May to Jun) changes (P < 0.05, Welch's t-test) are indicated by solid lines, and nonsignificant changes indicated by broken lines.

abundance in the treated lakes was consistently below 200 turions/m² and was less variable than in the reference lakes (Fig. 7 and 8).

Turion viability (% sprouted) did not change dramatically in treated or reference lakes in the monitored years but was generally lower in the treated lakes, particularly after the second year of treatment (Table 3). Turion viability in the treated lakes after the initial treatment year (66% ± 14% sprouted) was not substantially different than the 4-year mean of viability in the reference lakes (82 ± 4% sprouted, P = 0.08). Similarly, we did not see a substantial reduction of turion viability after the initial year of treatment in the one lake with pretreatment turion viability data (Rebecca, from 85 to 76%). In the subsequent years of treatment, however, mean turion viability in the treated lakes was lower than in the reference lakes (Y2 = 49% ± 12% sprouted, P < 0.001; Y3 = 53% ± 14%, P = 0.003; Y4 = 50% ± 20%, P = 0.03). Turion viability was highly variable among both the treated and reference lakes over the 4 monitored years, ranging from 12 to 83% in treated lakes and from 71 to 91% in untreated reference lakes, but was remarkably consistent within most

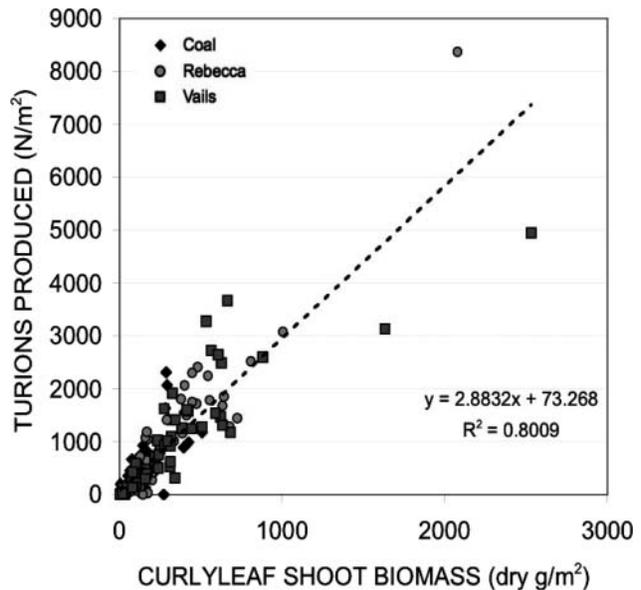


Figure 6.-Turion production vs. curlyleaf shoot biomass (turions excluded) in untreated reference lakes (June; 2006 to 2009).

Table 2.-Production of new curlyleaf pondweed turions (N produced/m²) in herbicide-treated lakes and untreated reference lakes in June 2006 to 2009; presented as littoral means ($\leq 4.6\text{ m}$) with one standard error (SE) given in parentheses. Results listed by treatment year for treated lakes (Y0 = pretreatment, Y1 = first year of treatment) and by calendar year for untreated lakes (treatment years not synchronized with calendar years).

	Herbicide-Treated Lakes										Untreated		
	Blueberry	Clear	Crookneck ^a	Fish ^a	Julia	Long	L. Mission	Rebecca ^c	Rush	Weaver ^b	Coal	Rebecca ^c	Vails
Y0 mean (SE)	—	—	—	—	—	—	—	313 (93)	—	2006	96 (47)	1871 (589)	360 (144)
Y1	—	—	<1 (<1)	—	0	—	0	11 ^c (4)	0—	—	312 (93)	778 (210)	509 (124)
Y2	1 (<1)	0	<1 (<1)	3 (2)	0	0	<1 (<1)	—	0—	0	87 (46)	313 (93)	379 (124)
Y3	1 (<1)	0	2 (2)	<1 (<1)	0	0	0	—	0—	0	52 (23)	—	206 (83)
Y4	—	—	8 ^a (5)	<1 (<1)	0	—	<1 (<1)	—	0—	0	—	—	—
Y5	—	—	—	10 ^a (8)	—	—	—	—	—	0	—	—	—

^aNot treated in 2009; 2009 values are included but represent data collected in untreated year

^bTreated for 5 consecutive years (2005–2009)

^cTreated for 1 year (2009)

Table 3.-Viability (% sprouted) and abundance of viable curlyleaf pondweed turions (N/m²) collected from littoral sediments (≤ 4.6 m) of herbicide-treated lakes and untreated reference lakes in October 2006–2009. Results listed by treatment year for treated lakes (Y0 = pretreatment, Y1 = first year of treatment) and by calendar year for untreated lakes (treatment years not synchronized with calendar years).

	Herbicide-Treated Lakes											Untreated		
	Blueberry	Clear	Crookneck ^a	Fish ^a	Julia	Long	L. Mission	Rebecca ^c	Rush	Weaver ^b	Coal	Rebecca ^c	Vails	
% Sprouted														
Y0 (pre)	—	—	—	—	—	—	—	—	—	—	2006	76	82	
Y1	—	—	73	—	81	—	59	76 ^c	43	—	2007	85	85	
Y2	41	30	74	29	77	40	45	—	62	42	2008	85	89	
Y3	57	44	76	50	83	12	52	—	63	40	2009	—	83	
Y4	—	—	69 ^a	40	76	—	21	—	67	45	—	—	—	
Y5	—	—	—	40 ^a	—	—	—	—	—	48	—	—	—	
Abundance of viable turions (N/m ²) ^d														
Y0 (pre)	—	—	—	—	—	—	—	—	—	—	2006	111	208	
Y1	—	—	85	—	27	—	103	725	25	—	2007	132	451	
Y2	176	41	115	55	22	54	67	330	20	79	2008	161	681	
Y3	88	53	75	22	17	5	88	—	30	54	2009	86	94	
Y4	—	—	30 ^a	38	14	—	12	—	7	71	—	—	—	
Y5	—	—	—	27 ^a	—	—	—	—	—	49	—	—	—	

^aNot treated in 2009; 2009 values are included but represent data collected in untreated year

^bTreated for 5 consecutive years (2005–2009)

^cTreated for 1 year (2009)

^dTotal Turion Abundance \times proportion sprouted

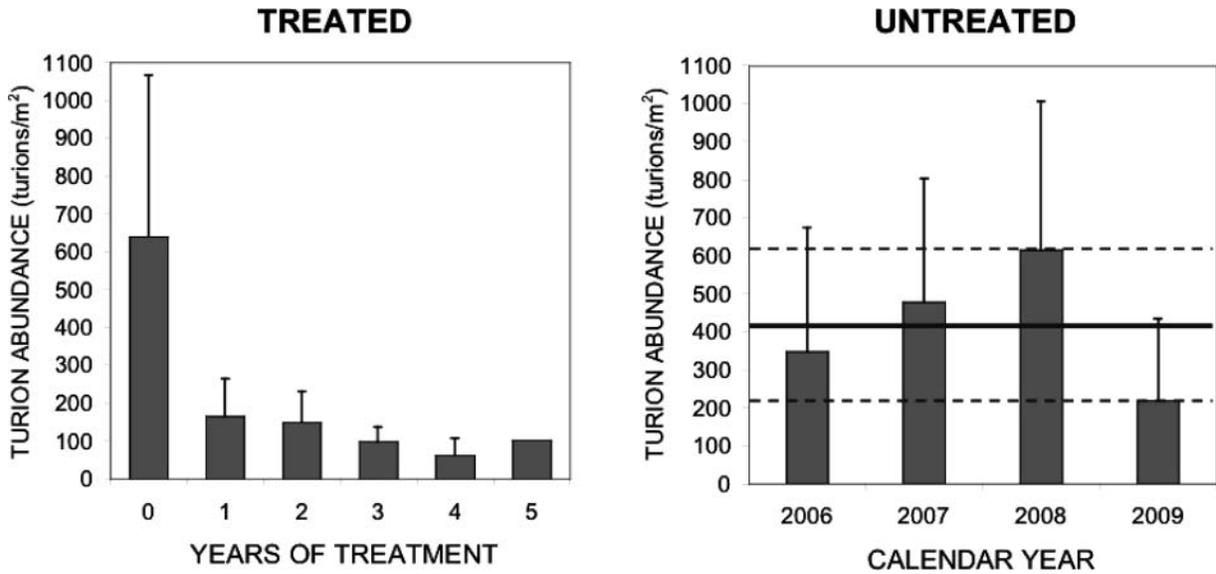
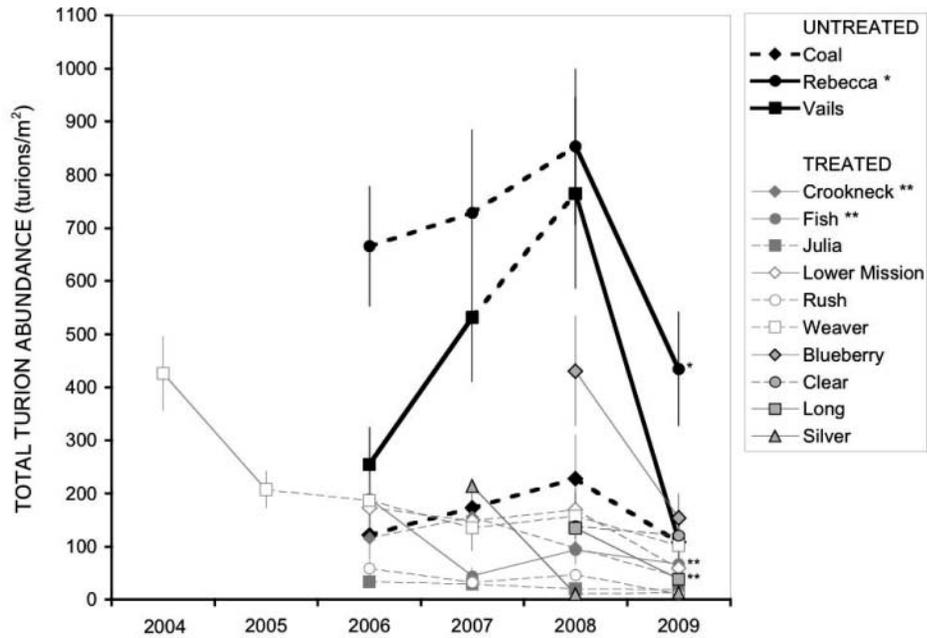


Figure 7.-Mean curlyleaf turion abundance (Oct, turions/m²) in littoral sediments (≤ 4.6 m) of treated lakes (by years of treatment) and untreated reference lakes (by calendar year). Error bars represent +2 SE. Horizontal lines represent the 4-year mean (solid) and 95% CI (dashed) for untreated reference lakes.



* Rebecca Lake (reference) treated in 2009 (grouped with treated lakes for 2009)

** Not treated in 2009

Figure 8.-Abundance of curlyleaf pondweed turions (sprouted + unsprouted) in littoral sediments (≤ 4.6 m) of herbicide-treated lakes and untreated reference lakes. Error bars represent ± 1 SE. Significant between-year changes ($P < 0.05$, Welch's t-test) indicated by solid lines; nonsignificant changes indicated by broken lines.

individual lakes (Table 3). Overall, these results suggest that the pool of turions that remained in the sediments of treated lakes after 2 or more years of treatment were somewhat less viable (or more deeply dormant) than the pool of turions in untreated lakes; however, the viability of these remaining turions did not seem to decrease after the initial 2 years of treatment (remained at ~50% viable).

The abundance of viable turions in treated lakes after the initial year of treatment (114 ± 112 turions/m²) was lower than the 4-year mean in reference lakes (368 ± 161 viable turions/m², $P = 0.03$). In the subsequent years of treatment, abundance of viable turions in treated lakes remained lower than in the reference lakes, with some indication of further decreases (Y2 = 70 ± 33 viable turions/m², $P = 0.005$; Y3 = 48 ± 21 /m², $P = 0.004$; Y4 = 28 ± 24 /m², $P = 0.002$).

Discussion

Curlyleaf frequency

Our results show that lakewide, early season, endothall and fluridone treatments substantially reduced curlyleaf frequency within each year of treatment (May to Jun). These results agree with those of Skogerboe et al. (2008), who also reported dramatic within-year reductions of curlyleaf frequency in 2 Minnesota lakes during each of the first 3 years of lakewide endothall treatment. Furthermore, our results suggest that multiple consecutive years of treatment provided some cumulative carryover reductions of curlyleaf frequency in lakes treated for 2 or more consecutive years. As a metric, frequency of occurrence is relatively insensitive to reductions in curlyleaf unless those reductions are large. This lack of sensitivity arises from frequency calculations based on presence or absence of curlyleaf at each sampled site regardless of the amount of curlyleaf found. Despite this insensitivity to reductions of curlyleaf, we observed decreased curlyleaf frequency in our treated lakes, indicating that the effects of herbicide treatments on curlyleaf frequency were substantial both within each treatment year (May to Jun) and between consecutive treatment years (May to May).

May curlyleaf frequency in the reference lakes was more variable between years than we anticipated. Much of this between-year variation was likely attributable to regional climatic differences that enhanced May curlyleaf growth in 2006 and 2007 and delayed curlyleaf growth in 2008 and 2009. Other studies have suggested that early season curlyleaf growth can be affected greatly by the availability of light during the winter (a function of snowfall and duration of ice cover) and spring water temperatures (Kunii 1982, Tobiessen and Snow 1984, Valley and Heiskary 2012). These weather-related conditions likely affected curlyleaf

growth similarly in both our treated and reference lakes (similar geographic locations), but due to the asynchrony of the initial treatments among treated lakes we were not able to discern weather effects from herbicide effects within individual treatment years. In grouping results from treated lakes according to the number of years treated, however, we incorporated data from across calendar years in each grouping. Consequently, the clear reduction of curlyleaf frequency in our treated lakes was likely attributable largely to herbicides effects rather than weather effects. Furthermore, curlyleaf frequency in the treated lakes after more than 2 years of treatment was significantly lower than in the reference lakes, despite the high amount of between-year variability in the reference lakes. Although these results clearly showed that herbicide treatments dramatically reduced curlyleaf frequency after multiple, consecutive years of treatment, curlyleaf was still present at low levels, even in lakes that received 4 or 5 consecutive years of treatment.

Curlyleaf biomass

Our results clearly show that early season herbicide treatments suppressed curlyleaf biomass within each year of treatment. Curlyleaf biomass in treated lakes remained low (generally <10 g/m²) in all treatment years, while curlyleaf biomass in reference lakes generally increased to much higher levels by June (~ 20 – 500 g/m²). Furthermore, we observed no surface-matted curlyleaf growth in treated lakes but encountered widespread dense surface-matted growth in reference lakes in June of all 4 monitored years. These results agree strongly with those reported by Skogerboe et al. (2008), who also found that curlyleaf biomass was suppressed in treated lakes during each year of lakewide treatment, while biomass in untreated lakes increased to nuisance levels by June. Similarly, Netherland et al. (2000) reported near complete within-year control of curlyleaf biomass in small pond cells treated with endothall.

Pretreatment biomass collected in May just prior to the initial treatments was low in our treated lakes. Consequently, we did not see a trend of decreasing curlyleaf biomass relative to pretreatment with successive years of treatment. May biomass in the treated lakes remained very low throughout our study, however, and was generally much lower than the May biomass in the reference lakes. In the reference lakes, May biomass was highly variable between years and seemed to be affected more than frequency by early season weather conditions. Skogerboe et al. (2008) similarly reported high between-year variability in early season curlyleaf biomass in both treated and reference lakes, suggesting that curlyleaf frequency may be a better metric than biomass for assessing early season carryover effects from previous years of treatment.

Variability of curlyleaf biomass among our reference lakes seemed to be related to the extent of curlyleaf growth (% occurrence) in each lake rather than localized differences in growth density. For example, Coal Lake had only a few large patches of dense curlyleaf growth (as evidenced by its lower % occurrence than in the other reference lakes) and thus had fewer littoral sites with high curlyleaf biomass. As a result, littoral means of curlyleaf biomass in Coal Lake were substantially lower than the other reference lakes. By contrast, Rebecca Lake supported dense curlyleaf growth throughout most of its littoral area, and thus had higher mean curlyleaf biomass.

Curlyleaf turions

Our finding of greatly reduced turion production in treated lakes (>99% reduction compared to reference lakes) is similar to results reported by Poovey et al. (2002), who found a 90% reduction of turion production in endothall tank studies, and Netherland et al. (2000), who found an 86% reduction of turion production in treated pond cells relative to untreated cells. However, turion production in the reference lakes was quite variable both among lakes and between years. As seen with curlyleaf biomass, the between-year variability of turion production in reference lakes seemed to be related to regional climatic differences in each of the study years (low turion production in years with low biomass), while among-lake variability seemed to be more related to the extent of curlyleaf growth in each lake. Our sampling methods also may have contributed to the variation we saw in turion production. Some new turions are only lightly attached to standing plants and may be easily detached during field collection and sample processing. Our method for collecting newly produced turions (collection of standing plants with a biomass rake) may have missed new turions that had already dropped from plants or may have knocked off turions that were very lightly attached to plants at the time of collection.

Overall, our estimates of turion production in untreated reference lakes (~50–1900 turions/m²) were generally lower than those reported by Bolduan et al. (1994; 900–1000 turions/m²) and Woolf and Madsen (2003; 700–2700 turions/m²). These discrepancies in the number of turions produced per square meter can be largely explained by considering that the values reported in these other studies reflected turion production in dense stands of curlyleaf growing in shallow water (<2 m), whereas our values represented littoral means. Our littoral means incorporated data from many sites with a wide range of curlyleaf densities, including samples from sites with no curlyleaf growth and deeper sites with little or no turion production on standing plants. Similarly, the percentage contribution of turions to total curlyleaf biomass in our reference lakes (9%) was substantially lower than the percentages reported by Rogers and

Breen (1980; 23% of total biomass), Kunii (1982; 42%), and Woolf and Madsen (2003; 22–58%) from untreated lakes, and our estimate of the number of turions produced per dry gram of curlyleaf shoot biomass in reference lakes (2.9 turions/dry g) was about one-half of that reported by Kunii (1982) from untreated lakes (~6 turions/dry g, estimated from plotted data). However, the mean dry mass of individual newly-produced turions in our reference lakes (43 ± 4 mg/turion) was fairly similar to the 53 mg/turion reported by Kunii (1982).

Given the nearly complete inhibition of turion production in our treated lakes and the continued sprouting of turions in each year, we expected to see continuing, substantial reductions in the abundance of turions in sediments of treated lakes over multiple, consecutive years of treatment. Although our results indicated that turion abundance in treated lakes declined substantially in the initial 1 or 2 years of treatment (~50% reduction), the rate of turion depletion slowed greatly in the subsequent treatment years and fairly high numbers of turions remained, even after 4 to 5 years of treatment. For most of our study lakes, we did not collect turion samples prior to the first year of treatment (only collected in Weaver and Rebecca). Although our results strongly suggest that turions decreased substantially in the initial year of treatment, future evaluations of such treatments should measure turion abundance in the fall prior to the initial treatment or in the early spring just prior to herbicide application.

In reference lakes, turion abundance in sediments was much more variable between years than anticipated, suggesting that differences in weather or in-lake conditions affected the amount of turion production or sprouting that occurred in each year, as suggested by Sastroutomo (1980, 1981) and Kunii (1982). From a management perspective, this suggests that herbicide treatment in years with enhanced turion sprouting would likely result in the greatest reductions of turion abundance (through sprouting without replacement). Mean turion abundance in our reference lakes (~100–850 turions/m²) was substantially lower than reported by Rogers and Breen (1980; 1320 turions/m²), Sastroutomo (1981; 2100 turions/m²), Bolduan et al. (1994; 1130 turions/m²) and Woolf and Madsen (2003; 1150 to 3030 turions/m²). As noted in our assessment of turion production, however, the values reported in these other studies generally depicted turion abundance in sediments from shallow areas (<2 m) that had previously supported dense stands of curlyleaf with high turion production and deposition. In contrast, our estimates of turion abundance represented littoral means, and thus included samples from areas with little or no curlyleaf growth and fewer deposited turions.

Although we observed some reduction in turion viability over the initial 2 years of treatment, we did not see further

reductions of turion viability over the subsequent years of treatment (leveled off at ~50% viability). Given that turion production was nearly eliminated by herbicide treatments, the turions remaining in the treated lakes in each year were almost certainly produced prior to the initial year of herbicide treatment. Sastroutomo (1981) reported that older (brown) turions were less viable than newly produced (green) turions, suggesting that turion viability decreased over time; however, our results indicated that turion viability did not change dramatically with age. Instead, our results suggest that in the initial years of treatment, the most viable or shallowest buried turions were removed from the turion pool through sprouting without replacement, leaving only the less viable or more deeply buried turions. These remaining turions had not sprouted in previous years, suggesting that they may have been produced with lower viability or more quiescent dormancy than the turions that had sprouted. Conversely, these turions may have been highly viable when produced but were deposited in areas where the immediate environment was not favorable to sprouting due to isolation from sprouting cues (Sastroutomo 1981, Jian et al. 2003) or burial in anoxic sediments (Wu et al. 2009). The lack of further reduction in viability after the initial 2 years of treatment suggests that the viability of individual turions either declines slowly or remains stable until the turion sprouts or decays. Furthermore, our results suggest that burial of turions in lake sediments may play a role in maintaining both the abundance and dormancy of turions in treated lakes.

Turion viability was generally quite stable within each individual treated lake (after the initial year of treatment) and reference lake during the monitored period. Turion viability was much more variable among lakes than within lakes (Table 3), however, suggesting that conditions within each lake, such as sediment texture, sediment deposition rate, or the degree of sediment anoxia (Wu et al. 2009) may have affected the ability of each lake to accumulate and harbor viable turions.

Our methods for assessing turion viability relied on cold storage to break dormancy, as suggested by Rogers and Breen (1980) and Sastroutomo (1981); however, many of the turions that did not sprout within 120 d did not appear to be decayed. These remaining unsprouted turions may have been deeply dormant rather than inviable. Consequently, the viability values we have reported should be considered minimum estimates of turion viability.

Management implications

The use of herbicides to control curlyleaf pondweed is not a new idea; however, in the past, the vast majority of such treatments in northern states have focused on reducing curlyleaf biomass in localized areas (not lakewide) with herbicide

applications that occurred later in the spring and at higher concentrations than in our study. Our results show that early season, low-dose treatments can effectively control curlyleaf biomass on a lakewide scale while also inhibiting the production of new turions and reducing the abundance of viable turions in lake sediments. Although only one of our study lakes was treated with fluridone (Weaver), we saw no substantial difference in the degree of curlyleaf control offered by endothall or fluridone in our study lakes. These findings strongly suggest that the previously reported effectiveness of cool-water, low-dose herbicide treatments for controlling curlyleaf in aquarium and pond studies (Netherland et al. 2000, Poovey et al. 2002) can also be achieved in larger lakes.

The greatest reductions in curlyleaf frequency, biomass, and turion abundance seemed to occur in the first 2 consecutive years of treatment; however, we saw additional smaller reductions of curlyleaf frequency and turion abundance in lakes with more than 2 consecutive years of treatment. From a management perspective, this suggests that any lakewide treatments for curlyleaf should be repeated for at least 2 to 3 years, but additional years of lakewide treatment may not provide a substantial amount of additional control.

Previous studies have suggested that the rapid senescence and decay of curlyleaf pondweed during the late spring may contribute to internal nutrient recycling in heavily infested lakes (Bolduan et al. 1994, James et al. 2002). Lake managers have further speculated that such augmentation of internal nutrient loading by curlyleaf may lead to more frequent or more severe algae blooms and a decrease in water clarity. Consequently, many large-scale curlyleaf control projects in the upper Midwest have been motivated or justified as a way to decrease nutrient concentrations and increase water clarity in infested lakes. Water clarity in our treated lakes generally did not change more than in untreated reference lakes, and there was no clear trend of increasing water clarity in most of our treated lakes (Table 4). Weaver Lake was a notable exception, showing a 150% increase in late summer (Jul and Aug) water clarity (increased from 0.8 m pretreatment to 2.0 m posttreatment). We did not monitor nutrient loading or nutrient concentrations in our study lakes, so we were not able to discern the effect of curlyleaf control on nutrient loading; however, our results suggest that in many lakes, lakewide control of curlyleaf may not lead to increased water clarity. Additional detailed studies are needed to further explore the effects of curlyleaf control on nutrient loading and water clarity.

Although we observed decreased turion abundance in our treated lakes, we found no clear indication of a critical number of treatment years needed to achieve long-term control of curlyleaf (nearly complete depletion of turions in sediment). Considering that turion production was inhibited

in our treated lakes, the continued, widespread but sparse sprouting of curlyleaf we observed after 4 to 5 years of treatment suggested that additional turion depletion was still occurring in the later years of treatment but at a much lower rate than during the initial few years of treatment. However, the persistence of viable turions and lack of declining turion viability after 4 to 5 consecutive years of treatment suggests that total depletion of turions would require substantially more than 5 consecutive years of treatment and may not be a realistic goal.

Currently, the link between the abundance of buried, viable turions in lake sediments and the level of curlyleaf sprouting after lakewide herbicide treatments are stopped is not well understood. Two of our study lakes (Crookneck and Fish; previously treated for 3 and 4 years, respectively) were not treated in 2009. In that year, these 2 lakes experienced small but significant increases in curlyleaf frequency between May and June (increased by ~10% occurrence compared to May of previous year), but frequency in these lakes remained much lower than seen in May of the initial year of treatment (~40–60% occurrence; Fig. 3). Furthermore, curlyleaf biomass and turion abundance in these 2 lakes did not increase significantly in 2009 (Fig. 5 and 8), suggesting that after 3 to 4 consecutive years of treatment, these lakes experienced at least one year of reduced curlyleaf (relative to pretreatment conditions) after treatments were stopped. Although the results from these 2 lakes are promising, the increase in curlyleaf frequency in 2009 (untreated year) shows that curlyleaf will almost certainly recover in treated lakes if left unmanaged. Additional work is needed (1) to determine how long buried turions can remain viable in lake sediments, and (2) to assess the rate of curlyleaf reestablishment from different levels of turion abundance in previously treated lakes. A better understanding of these factors would allow optimization of treatment strategies to provide the greatest reduction of nuisance curlyleaf growth while minimizing the cost of treatment programs and potential impacts to native aquatic plants.

Although the research presented here focuses on the effects of herbicide treatment on curlyleaf pondweed, the goal of these treatments was to control curlyleaf while simultaneously protecting or enhancing the native plant community. Assessments of the native plant communities in our study lakes indicated that the frequency and abundance of native plant were not reduced by lakewide, early season endotherm treatments (Jones et al. 2012); however, we did see shifts in the dominance of some native plant taxa in treated lakes (detailed evaluation of native plant community response in our treated lakes in Jones et al. 2012).

The persistence of buried, viable turions and the possibility of additional low levels of sprouting from deposited curlyleaf seeds suggests that eradication of curlyleaf may

not be feasible using herbicides. If future research determines the length of time that buried turions can remain viable, our results indicate that early spring treatments could effectively inhibit turion production for that length of time. Alternatively, if the sprouting of buried turions could be enhanced, lakewide treatments could be used to prevent new turion deposition and lead to substantial depletion of the pool of turions. Although eradication may not be feasible, our results indicated that herbicide treatments can effectively reduce severe infestations of curlyleaf to a point where less intensive control measures, such as localized spot herbicide treatments and small-scale harvesting or cutting (Deschenes and Ludlow 1993, Madsen 2000) may be able to maintain effective control of nuisance curlyleaf growth.

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